

Choreography of the Squid's "Nuptial Dance"

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*A mass spawning of squid resembles, at first glance, a chaotic "nuptial dance" (1). But for the first time, we have applied 3-D, radio-linked acoustic positioning (RAP) to this confusing process, and our early results now reveal a choreography that is, in fact, well organized in time and space. Remote tracking with RAP of individual *Loligo vulgaris reynaudii* off South Africa has provided insights into the daily sequence of behaviors that lead these animals to aggregate for sexual selection. Each dawn, the squid navigate for several kilometers, toward the shore, to small, well-defined zones near egg beds on the substrate. After several hours of circling above these egg beds, a pelagic, 3-D lek-like aggregation of large males forms; females are drawn in, and the aggregation condenses as the females and males pair, mate, and lay eggs. Smaller "sneaker males" remain on the periphery of the mating arena and, from this station, attempt extra-pair copulations (EPCs). The mating system of squids is thus unexpectedly complex, rivaling those of mammals and birds (2, 3). Commercial squid-jigging fishermen in South Africa have recently been attracted to the spawning grounds, and they have been successful. Moreover, their activities may be selective for large males. Thus, attention should be devoted to ensuring that such targeted fishing does not alter the characteristics of squid population genetics. Remote tracking and video observations, in combination with genetic analyses, may offer a new opportunity to monitor mating effort and reproductive success, and thus to manage the fishery.*

Determining the reproductive behavior of highly mobile marine animals is challenging, but the results can be rewarding, particularly in situations in which the species

is the target of a fishery that is conducted directly on the spawning grounds. Collaborative efforts between the fishermen's cooperatives and the government's Sea Fisheries Research Institute led to the present study, which was conducted in November 1993 and November 1994 in Oyster Bay, South Africa. Underwater visibility was limited and diving conditions were treacherous, thus the observations of squid behavior by divers during these periods were substantially complemented by an analysis of data collected by remote tracking.

Eight squid were fitted with acoustic transmitters that produced pulses of 50–80 kHz "pings." The devices were placed within the mantle cavity and attached to the mantle wall by a hypodermic needle that was thrust through the wall, crimped, and secured with silicone washers (see 4). Four of the eight squid were large males (430 g; mantle length [ML] about 32 cm), two carrying Vemco V16T-3H telemetry tags with a thermistor-controlled pulse interval, one a V16-3H pinger (all, 70 × 16 mm diameter), and one a V8-2L pinger with a constant pulse interval of about 1 s (35 × 8 mm diameter). These transmitters encoded temperatures in the intervals between pings (as the data on depth and jet pressure had been telemetered in previous studies; 4). In addition, two small "sneaker" males (70 g; about 15 cm ML) and two females (180 g; about 21 cm ML) each carried V8-2L pingers. The data supplied by all of these transmitters are equivalent to those provided by long-term, focal sampling of animal behavior (5).

The acoustic transmitters borne by the squids were tracked for 14 days by four hydrophone-equipped RAP buoys (Vemco Ltd., Shad Bay, NS, Canada) moored in Oyster Bay in a 45-m square over two small egg beds (each about 1 × 2 m) located 1 km offshore. The buoys monitored the arrival times of signals from the tagged

squid and transmitted them by radio to a base station, which used a triangulation routine (6) to calculate 3-D positions. The eight squid were tracked for a total of 54 animal-days (maximum for one individual, 14 d). They produced 35 megabytes of positional data, and the four large male squid produced temperature data as well.

Data from transmitters fixed to the substrate were compared with data from diver-transported units so that the accuracy of the software in its present state of development could be evaluated. These tests showed position accuracy of less than 1 m inside the array of RAP buoys, decreasing to 5–10 m at a 150-m radius from the center of the array (note Fig. 2). Full resolution of point-by-point tracks requires a complex post-analysis that is still in progress, but 10–20 s averaging gave reasonable, real-time tracks for typical squid speeds of 10–50 cm s^{-1} . At worst, a squid moving 50 cm s^{-1} , signaling its position every 20 s, produces points 10 m apart at 150 m from

the center of the array; smaller movements are usually recorded at slower speeds.

The eight squid being tracked were consistently present near the array during the day. The diel rhythmicity with which the three types of squid appeared on the egg beds is illustrated in Figure 1. These behavioral observations are limited in number, but they are consistent; this consistency, together with our previous experience (4), indicates that acoustically tagged squid show the normal range of movement.

At dawn, the squid arrived in the vicinity of the egg beds. The large males made circles (50–150 m radius) around the area (records of these and subsequent movements are shown in Fig. 2). Females and other males gradually joined the large males as they coalesced into a 3-D mating arena that was generally situated within 10 m of the substrate (typical depths were 20–30 m). Agonistic behavior among males was very striking and

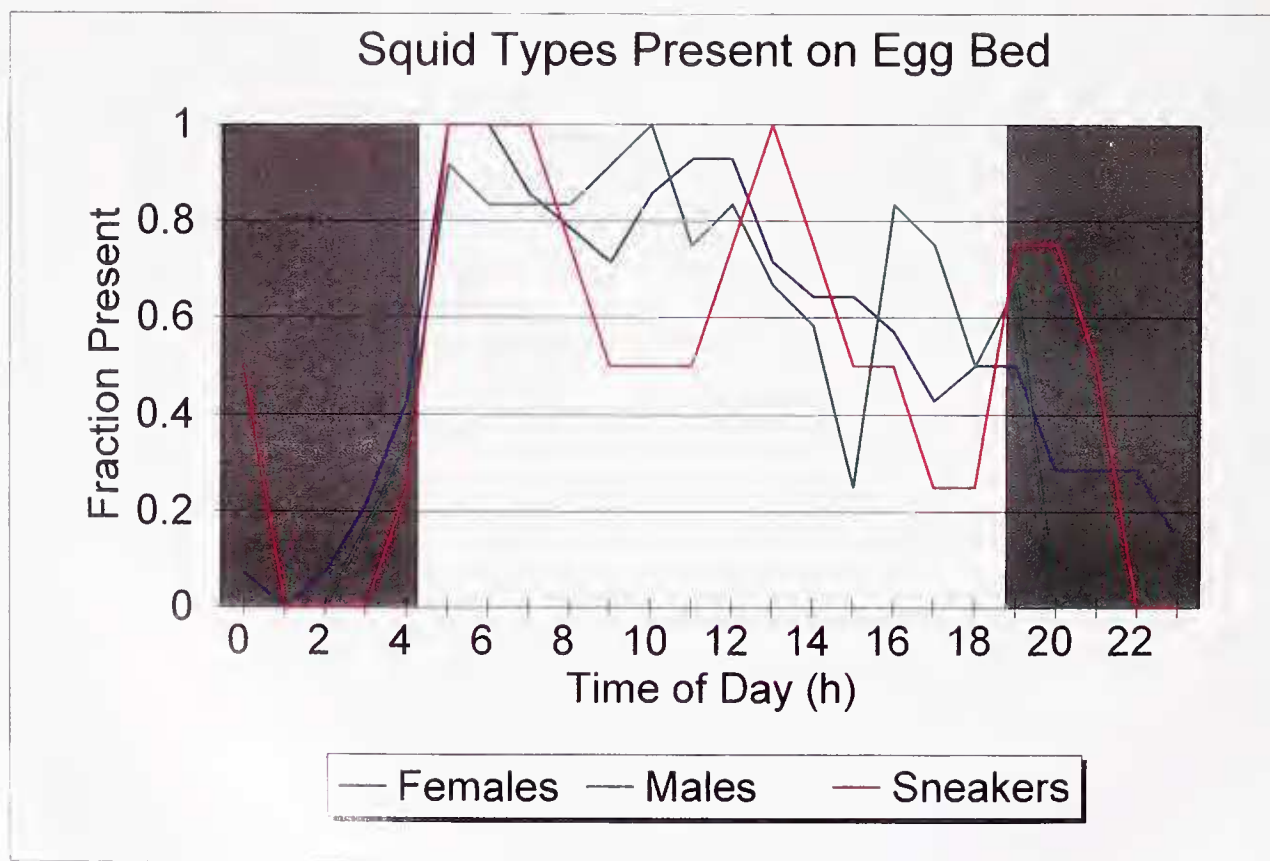


Figure 1. Diel patterns of squid visitations to the egg bed, shown as the ratio of hours present to hours monitored. Three large males (blue, 32 cm mantle length) were monitored over 8 full days, two females (green, 21 cm ML) over 7 days, and two small "sneaker" males (red, 15 cm ML) over 2 days. Females and sneakers from offshore appear at dawn and often remain past dusk. Large males also appear at dawn, although numbers peak later; they often disappear by noon and make brief return visits before moving offshore at dusk. A trade-off between detailed tracking of individuals and continuous monitoring of all frequencies makes statistical analysis of daytime data difficult, but continuous monitoring at night (1800 h–0400 h) did not indicate the presence of large males or females, so patterns are clearly distinct.

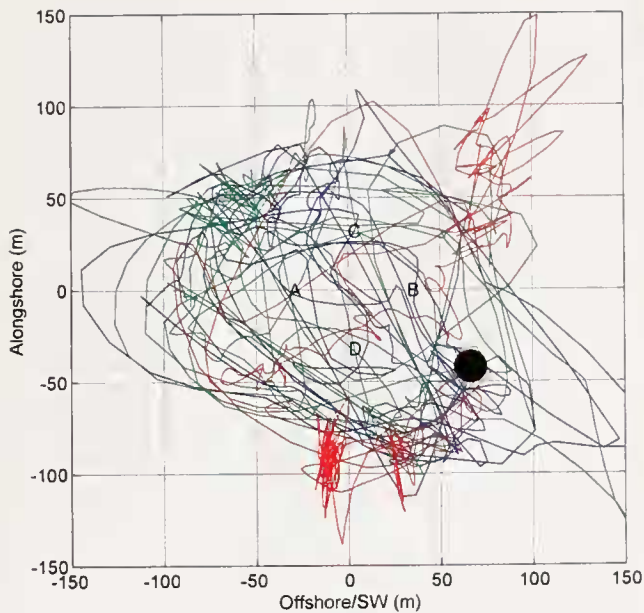


Figure 2. Overhead view of a typical full day of tracks for a large male (blue), a female (green), and a sneaker male (red); full details of behaviors can be replayed on computer animations. The black dot identifies an egg mass confirmed by divers; video surveys also showed numerous squid and scattered egg fingers beneath the area of heavy tracks on the opposite side of the array. Ten days of similar records show that males and females begin at dawn making circles of 50–150 m radius, high in the water column, around the sonobuoy array (A,B,C,D). Circling decreases by mid-morning, and in the afternoon females spend more time near bottom at individual egg patches. Sneaker males remain outside the main arena, low in the water column and near egg patches; direct observations show that they rush in to intercept pairs. Speeds average 18 cm s^{-1} for females, 14 cm s^{-1} for large males, and 17 cm s^{-1} for small sneakers.

common as they competed for temporary pairings with females (7: unpubl. results). The paired large males and females mated, and the female then moved with her partner to the substrate to deposit her "egg fingers" (Fig. 3). Although these squid need adjacent bottom for egg-finger attachment, criteria for such beds are not stringent. Lone large males often waited near the egg beds to intercept pairs moving to and from the communal egg beds.

This activity—repeated mating and egg laying with a series of temporary partners—often continued for 1–2 h after sunset (Fig. 1). Meanwhile, the sneaker males remained all day at the periphery of the arenas (Figs. 1 and 2). In this station, presumably, they are maximizing their opportunities for extra-pair copulations (EPCs): that is, watching for females temporarily paired with larger males; then, after the pair has mated, swimming rapidly into the arena to mate briefly with those females (Fig. 4). The mean duration of a sneaker male's mating was only 6 s; in contrast, large males mated for 16–20 s (7). Large males occasionally left during the day, and one



Figure 3. Photo of a large male escorting a female squid (*Loligo vulgaris reynaudii*) as she attaches an "egg finger" of about 100 eggs to an egg bed. Photo by MJS.

was tracked manually by boat to another mating arena 1.5 km alongshore. Tagged large males were apparently unsuccessful in mating, as evidenced by the short time they spent near the egg beds. In contrast, paired males escort female mates to the egg beds and guard them as their eggs are deposited (Fig. 3). This does not necessarily imply that tags interfered with normal behavior, because males outnumber females.

Most squid moved offshore at dusk; one large male was tracked 2 km offshore, where he remained relatively stationary (perhaps feeding or resting) until his return at dawn. During this male's onshore migration, his mean swimming speed was, as expected, 1 body length per second (45 cm s^{-1}), three times his speed in the mating arena. In contrast, sneakers were smaller and faster, averaging nearly 1 body length per second for the whole day; their tactic of avoiding large males and achieving sneak EPCs requires swift swimming.



Figure 4. This enhanced video image of a "sneaker" male (left) intercepting a temporary pair and attaching a sperm package to the female with no response by the escort (right) is direct evidence of sneaking in squid mating systems. Video by RTH.

Males of various terrestrial and aquatic taxa assemble in large leks or lek-like aggregations to attract females and then compete for mating access (2, 3, 8, 9). Among loliginid squids, however, the tactic that appears to be primary is the intensive sexual selection that occurs in these nearshore mating arenas, with many of the requisites for leks (2). We suggest that the daily offshore-to-inshore movements and circling aggregation of male squid draw in new male and female schools from offshore, increasing the size of the aggregation and the number of females. Our picture of the dynamics of these lek-like aggregations suggests that high-biomass mating arenas ensure that most eggs are deposited in locations with a high probability of hatching success. Other potential benefits of larger aggregations are more intensive competition for mates and more gene mixing in the population.

Overall, the squid mating system first includes a period of offshore mating that provides sperm to most females before the onset of the inshore migration. This sperm is stored and, as an alternative tactic, can be used by individual females that never make it to inshore mating arenas. Females that do participate in the inshore mating aggregations probably use the sperm of the large males with which they pair and mate in these arenas (10, 11). In the end, then, females that mate with large males and sneakers, as well as with males while offshore, have at least three sources of sperm (7, 11, 12). Therefore, the potential for genetic mixing—already increased by the spawning aggregation—will be further augmented. This type of mating system may be typical of loliginid squids, and assessment of paternity by some molecular technique will help resolve this possibility (12).

The fishery for the squid *Loligo vulgaris reynaudii* in South Africa began when fishermen located squid aggregations by sonar and jigged them intensively. At the outset, low-intensity jigging often yielded tons of squid daily for several months, primarily during what we now recognize as the early morning period of circling and pairing over mating arenas (13). Previous sporadic diving observations confirmed that the aggregated squid were spawning around communal egg beds (14, 15). At present fishing levels, the aggregations seem more transitory and isolated, and offshore spawning may have increased.

By now, the fishery, although relatively new, has become the third most valuable in South Africa (16); this fits the worldwide trend in which cephalopods have risen to third in dollar value (behind shrimp and tuna) as fin-fish stocks have declined due to fishing pressure (17). But this fishery clearly targets spawning squid. Therefore, fishery biologists and fisherman's cooperatives are keen to avert both biological and commercial disaster; thus they have been supporting the acquisition of baseline data on population dynamics, especially as it is influenced by reproductive behavior. Field trials combining molecular genetic and behavioral observations with ex-

perimental fishing are planned to develop management strategies that will avoid alteration or breakdown of the critical spawning aggregations. In addition to the potential for altering the mating dynamics (and thus gene distribution) on the mating arenas, recruitment could also be adversely affected by increases in the alternative tactic of mating and spawning offshore, where development temperatures and success may be lower (18).

The novel remote tracking project reported here is part of a larger program that includes videography of behaviors recorded by divers, analysis of the recapture of previously tagged squid, bottom surveys carried out by video using the Global Positioning Systems for location, and biomass assessments from sonar and trawl samples.

In summary, the use of an unorthodox technique (tagging and monitoring with RAP) led to the surprising conclusion that the squid's "nuptial dance" seems to be choreographed by the large males each morning, and that the nature of the interactions is reminiscent of lek aggregations of birds and mammals. Because the annual life cycle of squid is brief (19), and because the fishery has only recently developed, the system has great potential as a model of genetic shifts in populations that are subjected to natural selection from predators, sexual selection due to squid behavior, and selective fishing pressure from human behavior. Fishery managers might take advantage of this useful model system.

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